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Conspecific status of the sparid fishes Pagrus sedecim Ginsburg and Paqrus pagrus Linnaeus.
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Conspecific Status of the Sparid Fishes *Pagrus sedecim* Ginsburg and *Pagrus pagrus* Linnaeus

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Conspecific Status of the Sparid Fishes *Pagrus sedecim* Ginsburg and *Pagrus pagrus* Linnaeus

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The status of *Pagrus sedecim* Ginsburg, is reviewed. Specimens of eastern Atlantic *P. pagrus* were collected from the Canary Islands, Spain and those of *P. sedecim* were collected off North Carolina and the Gulf of Mexico during 1973–1974. Meristic counts, proportional measurements and muscle samples were obtained from the fish. Meristic and proportional measurement data were tested both arithmetically and by discriminant function analysis, and muscle samples were analyzed electrophoretically using regular disc gel and sodium dodecyl sulfate (SDS) methods.

Results indicate intraspecific differences. Therefore, *P. sedecim* is placed in the synonymy of *P. pagrus*, and eastern and western Atlantic porgies are considered to represent populations of a single species. Three hypotheses are proposed to explain the similarity of eastern and western Atlantic *Pagrus*. The hypothesis accepted states that although the populations have been separated a long time, sufficient gene flow has occurred to prevent divergence. Passive transport of larvae from Africa is considered a probable mechanism for maintaining gene flow between the eastern and western Atlantic stocks.

FISHES of the genus *Pagrus* are bottom dwellers associated with a variety of temperate to subtropical marine habitats. One species supports a large recreational fishery in the western Atlantic off the southeastern United States (Sekavec and Huntsman, 1973) and the others are commercially important fishes in Europe, Africa, and Asia. Presently five nominal species, three from the eastern Atlantic (*P. auriga* Valenciennes, *P. ehrenbergi* Valenciennes and *P. pagrus* Linnaeus), one from the western Atlantic (*P. sedecim* Ginsburg) and one Indo-Pacific species (*P. major* Temminck and Schlegel) are recognized.

Pagrus sedecim (Fig. 1) is distributed from North Carolina to Mexico and from Venezuela to Uruguay. The species has not been reported from the Caribbean or Central America. It was considered conspecific with the eastern Atlantic *P. pagrus* until Ginsburg (1952) compared 16 North American specimens to three from the Azores, and designated the western Atlantic

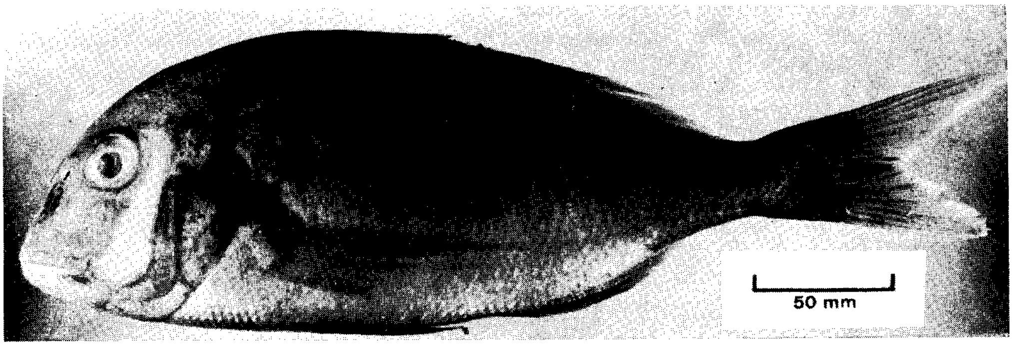

Fig. 1. *Pagrus sedecim* collected from the Gulf of Mexico, UNC 9535, 234 mm, SL.

form as a separate species, *P. sedecim*. Ginsburg's small sample sizes and our examination of specimens of *Pagrus* in the U.S. National Museum of Natural History prompted a review of the status of *P. sedecim*. Although we had ample material from the southeastern United States coast for the review, museum specimens of eastern Atlantic *P. pagrus* were scarce. The Sport Fishing Institute generously provided funds to support our collecting eastern Atlantic *Pagrus* (Fig. 2) in the Canary Islands, Spain in April 1974. These collections provided sufficient material to compare statistically the eastern Atlantic *P. pagrus* and the nominal western Atlantic *P. sedecim* utilizing a variety of meristic, morphometric and biochemical characters.

We are particularly indebted to David W. Frame who, before his untimely death, was instrumental in initiating the study. The Sport Fishing Institute provided financial assistance. The director, C. Garcia-Cabrera, and staff of the Laboratorio Oceanografico de Canarias, Tenerife, Canary Islands, provided laboratory space, living accommodations, and technical assistance; David R. Colby, Atlantic Estuarine Fisheries Center, National Marine Fisheries Service, developed statistical methods; and Paul J. Pristis, Gulf Coast Fisheries Center, National Marine Fisheries Service collected specimens from the Gulf of Mexico. Valuable laboratory work done by Robert L. Dixon, Atlantic Estuarine Fisheries Center, National Marine Fisheries Service is also appreciated. All photographs were taken by Herbert R. Gordy, NMFS.

Materials and Methods

Specimens were collected from three locations: Onslow Bay, North Carolina; Gulf of Mexico, Panama City, Florida; and Tenerife, Canary Islands, Spain, by employees of the National Marine Fisheries Service. The Canary Islands fish came from the municipal fish market at Santa Cruz de Tenerife, and were captured by handline from the Sahara Banks. These specimens, as well as the American fish, are cataloged in the University of North Caro-

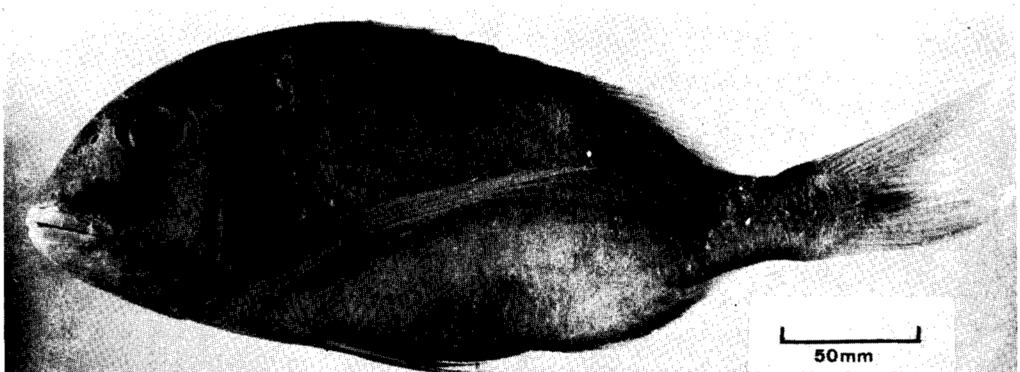

Fig. 2. *Pagrus pagrus* collected from Tenerife, Canary Islands, UNC 9534, 260 mm, SL.

lina Institute of Marine Science Museum (UNC 9534-9535). For each specimen, data were recorded on external meristics, vertebral counts and proportional body measurements. White muscle samples were obtained for biochemical analyses.

Several morphometric and meristic characters are used to distinguish the species of *Pagrus* (Fowler, 1936). The anterior dorsal spines of *Pagrus pagrus* are much shorter than those of other eastern Atlantic species (*P. auriga* and *P. ehrenbergi*). Ginsburg's (1952) separation of *P. sedecim* from *P. pagrus* was based on the number of pectoral rays, relative depth of the caudal peduncle, and differences in color of preserved specimens.

Most of our measurements and counts conform to those defined by Hubbs and Lagler (1958) with a few exceptions. The number of lateral line scales was counted from the edge of the gill opening to the base of the caudal fin, i.e., hypural plate. The several scales which extend posterior to the hypural were not counted. The posteriormost dorsal and anal rays, if bifurcate and not separated at the base, were counted as one. Total number of first-arch gill rakers included rudiments. The gill-raker counts were separated into the number for the upper limb of the arch, the single raker at the angle, and the count for the lower limb, in that sequence. Other measurements which require special definition are: length of pectoral fin (distance from base to longest tip); depth of body (from dorsal origin to just anterior to pelvic base); and head length (snout tip to posterior bony edge of opercle).

Proportional measurements used were: 1) body depth into standard length; 2) pectoral length into standard length; 3) head length into standard length; 4) eye diameter into head length; 5) nostril width into nostril length; and 6) standard length into peduncle depth.

Counts of vertebrae were made from diagnostic radiographs (Sutherland, 1958). Enumeration included all vertebrae between, but not including, the occipital and the hypurals.

Meristic and proportional measurement data were subjected to discriminant function analysis (Dixon, 1968).

For electrophoretic studies, white muscle tissue from individual fish was homogenized in 1½ volumes of buffer (0.3 M sucrose, 0.01 M triethanolamine). The homogenate was centrifuged for 20 min at 13,000 rpm (23,500 × g) at 4 C in a Sorval RC2B refrigerated centrifuge. The supernatant fluid was dialyzed vs. 20 volumes of distilled water at 4 C for 48 hours with several changes, and then centrifuged to remove the precipitated globulins.

Two types of electrophoretic procedures were used: regular disc gel electrophoresis, (Ornstein, 1964; Davis, 1964) and sodium dodecyl sulfate (SDS) electrophoresis (Weber and Osborne, 1969). For the latter technique, the incubation solution contained 6 M urea, the gels contained 5 M urea and 0.175 M EDTA, and the electrophoresis buffer contained 0.02 M EDTA. To increase resolution, the polyacrylamide concentration was increased to 10% in the SDS gels. All gels were stained with coomassie blue and destained by diffusion.

In addition to *P. pagrus* (17 specimens) and *P. sedecim* (28), electrophoeretic studies were conducted on nine other sparids: *Pagrus auriga* (7), *Pagellus acarne* (5), *Pagellus erythrinus* (7), *Pagellus mormyrus* (2), *Dentex filosus* (2), *Dentex macropthalmus* (7), *Diplodus sargus*, (5) *Calamus leucosteus* (1) and *Calamus nodosus* (1).

Results

Meristic Counts and Proportional Measurements.—Gulf of Mexico, Panama City, Florida, U.S.A. (n = 16). D. XII–XIII, 9–10; A. III, 8–9; LL 52–57 (Table 1); gill rakers 14–17 (Table 1); most frequently encountered sequence of first-arch gill-rakers 6 + 1 + 9; P. 15–16 (Table 1); vertebrae 24; branchiostegals 6. Body moderately deep, depth 2.52–2.75 in SL; pectoral fin 2.64–3.10 in SL; head 2.91–3.17 in SL; eye diameter 3.35–4.17 in head; nostril width 1.67–3.33 in nostril length; caudal peduncle depth 9.20–10.92% SL. Maxillary with cleft mid-laterally.

Onslow Bay, North Carolina, U.S.A. (n = 114). D. XII–XIII, 9–11; A. III, 7–9; LL 51–59; gill-rakers 13–17; most frequently encountered sequence 6 + 1 + 9; P. 15–16; vertebrae 24; branchiostegals 6. Body moderately deep, depth 2.44–2.93 in SL; pectoral fin 2.66–3.50 in SL; head 2.89–3.60 in SL; eye diameter 2.91–5.48 in head; nostril width 1.59–3.72 in nostril length; caudal peduncle depth 8.11–10.24% SL. Maxillary with cleft mid-laterally.

Canary Island, Spain (n = 57). D. XII, 9–10; A. III, 8–9; LL 51–56; gill rakers 14–17; most frequently encountered sequence 6 + 1 + 9; P. 14–16; vertebrae 24; branchiostegals 6. Depth of body 2.42–2.88 in SL; pectoral fin 2.59–3.10 in SL; head 2.76–3.41 in SL; eye diameter 2.77–4.70 in head; nostril width 1.05–4.25 in nostril length; caudal peduncle depth 8.82–10.42% SL. Maxillary with cleft mid-laterally.

TABLE 1. TOTAL NUMBER OF LATERAL LINE SCALES, FIRST-ARCH GILL RAKERS, AND PECTORAL RAYS IN *Pagrus* FROM THREE LOCATIONS.

	Lateral line scales										
Location	N	51	52	53	54	55	56	57	58	59	Mean
Gulf, U. S. A.	13		1		5	5	1	1			54.6
N. C., U. S. A.	66	3	3	16	7	18	10	8		1	54.5
Canary Is., Spain	51	1	3	15	15	15	2				53.9

	Total number of first arch gill rakers						
Location	N	13	14	15	16	17	Mean
Gulf, U. S. A.	16		2	5	6	3	15.6
N. C., U. S. A.	57	1	6	17	30	3	15.5
Canary Is., Spain	51		1	12	30	8	15.9

	Pectoral rays				
Location	N	14	15	16	Mean
Gulf, U. S. A.	16		3	13	15.8
N. C., U. S. A.	97		39	58	15.6
Canary Is., Spain	57	1	44	12	15.2

Vertebral Column.—In each fish x-rayed (31 from N.C., 16 from the Gulf of Mexico, and 45 from the Canary Islands), the vertebral column consisted of 10 trunk and 14 caudal vertebrae and 8 pairs of pleural ribs.

Coloration.—Both eastern and western Atlantic specimens were colored similarly, although the head of eastern Atlantic porgies was darker, particularly after preservation. Overall body color in life is reddish above and silver-white below. When stressed, fish become barred with 5 to 6 red, vertical bands. There are 11 to 12 rows of small blue spots occurring from the nape region to the caudal peduncle and extending ventrally to just below the base of the pectoral fin. Ventrally, the fish are white to gray-white. Jugular color varies from white to dark gray, and in older (larger) fish may be almost black. There are generally two light blue laterally directed streaks, one just above, and one just below the eye. The nostril and maxillary areas are silver-blue (metallic). The iris is yellow, the pupil black. Pelvic fins in life are light blue, but fade to white-gray upon death. Pectoral fins are light yellow. Caudal fin is also light yellow, shading to red at its posterior edge. Spiny dorsal fin is pink and the soft dorsal is yellow. Underwater, western Atlantic specimens appear uniformly silver-white with the blue spots evident. A dark band runs from just below the eye to the articulation of the jaw.

Preserved specimens appear dull, yellow-brown. The blue, red, and distinct yellow colors on the fins are lost. The spots are still visible, but are black or brown.

Statistical analysis of meristic and morphometric data.—Little difference in mean meristic and proportional values for eastern and western Atlantic porgies was noted. Only one mean meristic count, lateral line scales, varied even one whole unit (Table 1).

A discriminant function analysis of 11 characters was conducted to determine if these characters could readily distinguish the area of collection of a given specimen (Table 2). Initially, 16 variables were considered but five (dorsal and anal spines; total, trunk and caudal vertebrae) revealed no variation and were deleted from subsequent analysis. The remaining 11, when tested simultaneously, showed significant differences between samples from the three locations (Table 2), but only 64% of the North Carolina and 78% of the Canary Islands fish could be correctly identified from a mixed sample. In other words, the calculated discriminant function correctly classified only 64% of the North Carolina *Pagrus* in a mixed sample containing fish from North Carolina, the Gulf of Mexico and the Canary Islands. It appears that the test detected differences more characteristic of races or populations than of species. For instance, Fischler (1959) concluded that a discriminant

TABLE 2. MEAN MERISTIC AND PROPORTIONAL MEASUREMENTS OF ELEVEN CHARACTERS TESTED BY DISCRIMINANT FUNCTION ANALYSIS.

Character tested	Collection site N. C. (25)	Gulf (13)	Canary Is. (42)
Dorsal rays	9.96	9.92	9.98
Aanal rays	8.00	8.08	8.02
Pectoral rays	15.84	15.92	15.21
Lateral line scales	54.52	54.61	53.88
Gill rakers	15.60	15.61	15.93
SL/depth	2.70	2.64	2.67
SL/pectoral length	2.90	2.79	2.79
SL/head	3.15	3.01	3.15
Head length/ eye diameter	3.95	3.68	3.67
Nostril length/ nostril width	2.48	2.34	2.60
Caudal peduncle depth/SL	9.14	9.92	9.66

Chi-square: 138.0 ($p < .001$) with 22 d.f.

Fig. 3. Regular disc gels above, and sodium dodecyl sulfate gels below, of muscle extracts from *Pagrus sedecim*, *Pagrus pagrus*, and *Pagrus auriga* from left to right.

function analysis correctly identifying only 72% of the American shad (*Alosa sapidissima*) in a mixed sample was delineating races.

Because differences appeared to be less than species significant, we used Ginsburg's (1938) arithmetical method for classifying related populations. We selected two variables which showed the greatest variation between groups: pectoral rays and lateral line scales. We also used caudal peduncle depth, since Ginsburg used this character to distinguish *Pagrus sedecim*. North Carolina and Gulf of Mexico porgies were grouped together as a sample and compared with the eastern Atlantic sample. The three tests produced integration and divergence indices which are of race magnitude.

Although the heads of eastern Atlantic fish appeared in photographs to be somewhat deeper than those from the Gulf or North Carolina, measurements on heads of 15 specimens, five from each geographic location, failed to reveal substantial differences. Two morphometric ratios were evaluated: head length into head depth, and head length into distance from base of orbit to jaw articulation (depth of cheek). Mean values for the Canary Islands, Gulf, and North Carolina are: 0.8703, 0.8428 and 0.8821 for head length into head depth, and 0.2709, 0.2585 and 0.2829 for depth of cheek. There is more variation between western Atlantic samples than between the North Carolina and Canary Island samples.

Electrophoretic patterns.—Differing electrophoretic patterns theoretically denote genetic differences between samples. The protein banding patterns obtained by electrophoresis with the regular gel system were species specific except for the *Pagrus sedecim*–*Pagrus pagrus* species pair and the two *Calamus* species. The most prominent features of these patterns were the low molecular weight parvalbumins (Pèchere, Capony and Demaille, 1973). Variation in patterns within a species was observed and appeared to be an artifact resulting from freezing and thawing during shipment of the samples from the Canary Islands. SDS electrophoresis is insensitive to variations caused by freezing and thawing, but simultaneously, is less likely to detect low order taxonomic differences. Nevertheless, we found species specific patterns for all the forms studied except the two pairs *P. pagrus* and *P. sedecim*, and *Pagellus mormyrus* and *P. erythrinus*. By using both electrophoretic techniques we were able to distinguish all species studied except *P. pagrus* and *P. sedecim*.

Disc gels of muscle extracts from the three pagrids are represented in Fig. 3.

Discussion

Results of our analyses indicate that *Pagrus sedecim* is not a valid species and should be placed in the synonymy of *P. pagrus*. Ginsburg's (1952) small samples were insufficient to display the variation inherent in both eastern and western Atlantic populations.

Variation between different western Atlantic samples is likely to be as large as that between western and eastern Atlantic samples for most characters. Even the highly sensitive discriminant function analysis, which simultaneously employs several characters, was unable to furnish a clear-cut distinction of eastern and western fishes. The distinction allowed was on the basis of such small differences that they could not be designated of specific importance. Therefore, we consider the eastern and western Atlantic forms to represent populations of a single species.

It seems most likely that *P. pagrus* of the western Atlantic originated from west Africa. The genus *Pagrus* achieves its full Atlantic development there (three species) while only *P. pagrus* occurs in the western Atlantic. The North Equatorial Current could transport *Pagrus* eggs and larvae westward and deposit them in suitable habitat off northeast Brazil. The pelagic larval stage of *Pagrus* probably lasts long enough to effect this movement. Though larval longevity for *P. pagrus* is unknown, that for *P. major* in the Pacific is approximately 20 days and the fish are probably subject to passive transport until they are at least 50 days old. Additionally, the eggs are pelagic and float for 3 to 5 days before hatching.

Three hypotheses explaining the similarity of the eastern and western Atlantic fish are: 1) the forms are recently separated and have not diverged; 2) the forms have been geographically separated a long time, but there has been sufficient gene flow to prevent divergence; or 3) despite long geographic and genetic isolation, divergence has not occurred. Of these hypotheses, the second seems most likely, although the first has some merit.

We have no evidence to suggest recent addition of *Pagrus* to the western Atlantic fauna, unless it is the marked abundance of this fish off the south Atlantic and Gulf Coast (Sekavec and Huntsman, 1973; H. Austin, 19—). Population explosions are sometimes characteristic of recent invaders, such as the cattle egret, English sparrow and carp in the United States. Apparently *Pagrus* has occupied all suitable subtropical and warm temperate habitat from Cape Hatteras to Brazil. It seems to be well integrated into the diverse western Atlantic fauna, indicating a substantial residence time. As to the third hypothesis, the well developed diverse western Atlantic ichthyofauna (Briggs, 1974) would probably apply such concurrent competitive pressure that an immigrant species would rapidly change even though it possessed characters that slow evolution, such as long life span with repeated spawning, great mobility of adults, and a relatively long larval stage (Rosenblatt, 1963).

Instead, we believe that larval transport from Africa is sufficiently great to slow divergence of the two populations. It seems highly likely that *P. pagrus* came from Africa originally, and we consider it probable that the processes allowing the initial emigration continue.

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